

The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter

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Resting or basal metabolic rates, compared across a wide range of organisms, scale with respect to body mass as approximately the 0.75 power. This relationship has recently been linked to the fractal geometry of the appropriate transport system or, in the case of birds and mammals, the blood vascular system. However, the structural features of the blood vascular system should more closely reflect maximal aerobic metabolic rates rather than submaximal function. Thus, the maximal aerobic metabolic rates of birds and mammals should also scale as approximately the 0.75 power. A review of the literature on maximal oxygen consumption and factorial aerobic scope (maximum oxygen consumption divided by basal metabolic rate) suggests that body mass influences the capacity of the cardiovascular system to raise metabolic rates above those at rest. The results show that the maximum sustainable metabolic rates of both birds and mammals are similar and scale as approximately the 0.88 ± 0.02 power of body mass (and aerobic scope as approximately the 0.15 ± 0.05 power), when the measurements are standardized with respect to the differences in relative heart mass and haemoglobin concentration between species. The maximum heart beat frequency of birds and mammals is predicted to scale as the -0.12 ± 0.02 power of body mass, while that at rest should scale as -0.27 ± 0.04 .

Keywords: aerobic scope; oxygen consumption; scaling; heart mass; birds; mammals

1. INTRODUCTION

(a) General

Aerobic scope is a dimensionless ratio and is defined as the maximum oxygen consumption of an animal during exercise ($\dot{V}_{O_{2max}}$) divided by the minimum oxygen consumption at rest or basal metabolic rate (BMR). Thus, aerobic scope is an indication of the maximum sustainable aerobic ability of an animal when transferring from a resting to an exercising state. However, while aerobic scope is often referred to in the literature on birds and mammals (Hinds *et al.* 1993; Chappell *et al.* 1996; Jurgens *et al.* 1996; Bundle *et al.* 1999) there is little theoretical understanding of the relationship (if any) between $\dot{V}_{O_{2max}}$ and BMR. In particular, it is unclear exactly how differences in body mass between species may influence the values for $\dot{V}_{O_{2max}}$ and BMR and, hence, the allometric scaling of the capacity for aerobic scope. If $\dot{V}_{O_{2max}}$ and BMR scale with the same exponent with respect to body mass then the capacity for aerobic scope will be a biological constant.

BMR is usually taken to be the oxygen consumption of an unfed (post-absorptive) animal resting in the dark, in air and at a thermoneutral ambient temperature. Measurements of BMR have been made for hundreds of species of birds and mammals and, when plotted against body mass (M_b), have been shown to scale as *ca.* $M_b^{0.75}$ (Kleiber 1961). This interspecies scaling exponent of 0.75 for BMR appears to apply to almost all living organisms and has recently been theoretically linked to the fractal

geometry of the appropriate transport system or, in the case of birds and mammals, the blood vascular system (West *et al.* 1997). However, BMR represents an extremely low level of cardiovascular functional performance whereas the structural morphology of the respiratory and cardiovascular systems would be expected primarily to reflect the maximal aerobic function, in which case it would be anticipated that $\dot{V}_{O_{2max}}$ should also scale as *ca.* $M_b^{0.75}$ and that the capacity for aerobic scope should be independent of body mass.

Humans exhibit a wide range of values for $\dot{V}_{O_{2max}}$ and aerobic scope between different individuals and between different athletic disciplines. Aerobic scope can vary from around 12-fold in untrained males, through 16- to 21-fold for footballers and cyclists, respectively and up to around 24-fold for long-distance runners and cross-country skiers (Åstrand & Rodahl 1986). Evidently, this is the result of athletes having different degrees of investment in the peripheral and central structural adaptations required to support aerobic metabolism (Åstrand & Rodahl 1986; Shephard & Åstrand 1992). These differences in structural adaptations can also be used to make comparisons of aerobic athletic ability between different species of animals (Taylor & Weibel 1981; Weibel *et al.* 1991). However, while BMR appears to be greatly dependent on the overall body mass of a particular species (Kleiber 1961; Scott *et al.* 1996), $\dot{V}_{O_{2max}}$ is primarily dependent on the development of specialized structural adaptations such as the lungs, heart and mitochondria, the volumes of which are only indirectly associated with body mass

(Weibel *et al.* 1991; Bishop 1997). Thus, differences between species in their ability to perform sustained aerobic locomotor activity may have the potential to cause significant variance around any general line for the allometric scaling of $\dot{V}_{O_{2\max}}$ and, therefore, aerobic scope with respect to body mass.

I suggest that the interspecies variance in the structural investment for $\dot{V}_{O_{2\max}}$ among birds and mammals is so great that it may obscure the effect of body mass on the scaling of $\dot{V}_{O_{2\max}}$ and, hence, the capacity for aerobic scope. Normalizing the data for $\dot{V}_{O_{2\max}}$ with respect to species-specific structural investment for aerobic capacity should reveal the underlying influence of body mass on the aerobic capacity of the cardiovascular system. The aim of this paper is to estimate the scaling of $\dot{V}_{O_{2\max}}$ and the aerobic scope of birds and mammals by calculating the allometric scaling function for $\dot{V}_{O_{2\max}}$ and BMR of 'standard' animals which I will define as having a relative heart mass of 1% of body mass and a haemoglobin concentration of 15 g 100 ml⁻¹ blood (see § 2(a)).

(b) $\dot{V}_{O_{2\max}}$ and the aerobic scope of mammals and birds

There is relatively little evidence to indicate whether the $\dot{V}_{O_{2\max}}$ of mammals scales with a similar exponent to BMR (i.e. around 0.75), although the consensus view (either explicitly stated or implied) is that it does (Hemmingsen 1960; Taylor *et al.* 1981; Schmidt-Nielsen 1984; Bundle *et al.* 1999). In a review of the scaling of morphological and physiological variables in animals, Schmidt-Nielsen (1984) concluded that mammals in general have an aerobic scope of around tenfold and that this is likely to be independent of body mass, while a few highly selected species such as dogs and horses may have much higher values (i.e. > 30-fold). Schmidt-Nielsen (1984) relied primarily on the most comprehensive single data set available, which was that of Taylor *et al.* (1981) who studied the $\dot{V}_{O_{2\max}}$ of 21 species of wild and domestic mammals running on a treadmill (ranging from ca. 8 g to 200 kg body mass).

The study by Taylor *et al.* (1981) demonstrated the difficulty of interpreting the data for $\dot{V}_{O_{2\max}}$ and body mass (figure 1). The overall allometric scaling relationship was $\dot{V}_{O_{2\max}} = 115 M_b^{0.809 \pm 0.062} \text{ ml min}^{-1}$ and this exponent was not considered to be significantly different from the allometric scaling exponent for BMR. However, the equations applied separately to the 14 wild species and seven domestic species were $116 M_b^{0.790 \pm 0.048}$ and $101 M_b^{0.855 \pm 0.244}$, respectively, while the addition of 23 values from the literature gave a new overall allometric scaling relationship of $100 M_b^{0.845 \pm 0.030}$. None of these relationships were significantly different from each other due to the high variance within the data sets. Taylor *et al.* (1981) declined to favour the latter equation, although the exponent was likely to be significantly different from that of BMR, as they considered that the increase in the body mass exponent was due to a systematic error. Most of the additional data represented studies of small animals exposed to the cold and were ca. 20% lower than the $\dot{V}_{O_{2\max}}$ that would have been obtained using animals running on treadmills. Instead, they preferred the exponent for the wild animals ($M_b^{0.790 \pm 0.048}$) and excluded the data from the domestic animals. This was because the

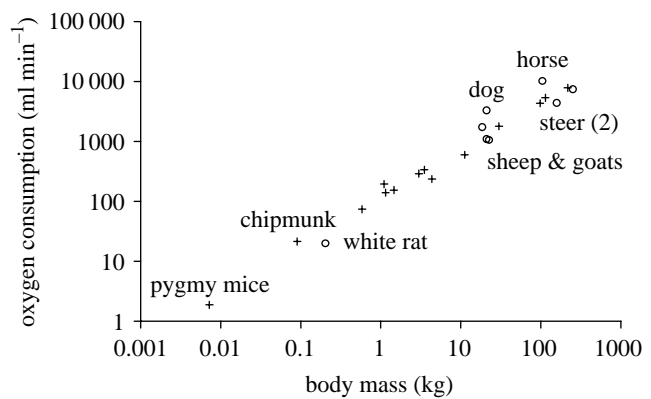


Figure 1. $\dot{V}_{O_{2\max}}$ plotted against body mass (kg) for 14 species of wild animals (plus signs) and seven species of domestic animals (open circles) running on a treadmill. Two values for the steer are given due to the large differences in body mass. Data taken from Taylor *et al.* (1981).

data from the domestic animals showed extreme variability between relatively athletic animals such as horses and dogs and relatively sedentary animals such as cattle, sheep and goats. More recently, Weibel *et al.* (1991) used a similar source of data and calculated that $\dot{V}_{O_{2\max}} = 106.8 M_b^{0.864 \pm 0.116}$.

However, the scatter in the data along the allometric line for $\dot{V}_{O_{2\max}}$ with respect to body mass is largely due to differential investment by the various species in the morphological adaptations required for aerobic metabolism (Weibel *et al.* 1991). Thus, a different type of systematic bias is introduced if there are not approximately equal numbers of relatively athletic and sedentary species included in the analysis and, in addition, if these two types of modalities are not evenly distributed with respect to body mass. One way of avoiding this type of error would be to include only examples of one type of modality or the other, but how should sedentary and athletic modalities be defined? For example, very small species of animals tend to be difficult to categorize in terms of their relative athletic ability (e.g. chipmunks or pygmy mice), although few would probably be considered sedentary. Yet most small terrestrial mammals have very limited aerobic capacities compared to those of bats and the latter were not considered by Taylor *et al.* (1981) and Weibel *et al.* (1991).

The information available for the scaling of the $\dot{V}_{O_{2\max}}$ of birds is even more limited than that for mammals (Bishop 1997). Schmidt-Nielsen (1984) again concluded that the aerobic scope of birds is probably a constant, but that the general value measured for birds during flight is slightly greater, at around 15-fold, than that of the general value for mammals while running (i.e. approximately tenfold). However, a recent study has shown that the rhea (21.8 kg body mass), a member of the flightless ratite group of birds, has a very large $\dot{V}_{O_{2\max}}$ and a reported aerobic scope of 36-fold (Bundle *et al.* 1999), which is around 1.5 times greater than that recorded for any other species of bird. Should this value for the flightless rhea be considered typical of birds in general or exceptional? Similarly, what about the values for the aerobic scopes of both wild and domestic dogs (Langman *et al.* 1981; Longworth *et al.* 1989) which are similar to

that of the rhea (i.e. around 30-fold) or for the domestic horse and the wild pronghorn antelope which have aerobic scopes of approximately 65-fold (Jones *et al.* 1989; Lindstedt *et al.* 1991)?

It would appear that larger species of relatively aerobic birds and mammals (e.g. body mass > 10 kg) are capable of evolving aerobic scopes greater than the figure of around 15-fold commonly attributed to birds during flight (body mass < 1 kg). Thus, the question as to whether aerobic scope scales independently of changes in body mass remains unclear, although it is fundamental to understanding the evolutionary constraints on the development of sustainable locomotor performance. However, the question itself is misleading and would be more useful if rephrased as 'Does body mass influence the capacity of the cardiovascular system to increase an animal's maximum metabolic rate above that of BMR, all other things being equal?' As mentioned above, in order to visualize the underlying influence of body mass on the aerobic capacity of the cardiovascular system, it is first necessary to standardize the data for $\dot{V}_{O_{2max}}$ and aerobic scope with respect to the relative species-specific differences in structural adaptations for aerobic metabolism.

2. THE $\dot{V}_{O_{2max}}$ AND AEROBIC SCOPE OF STANDARD BIRDS AND MAMMALS

(a) General methodology

The principle of symmorphosis (Taylor & Weibel 1981) suggests that, at any point along a physiological pathway, the maximum functional capacity of that point should be matched to the maximal functional capacity at any other point along the same pathway. This principle has been shown to be applicable to the structural and functional adaptations of the cardiovascular system of mammals, excluding the adaptations of the lung (Weibel *et al.* 1991). Thus, in general, it is only necessary to quantify the appropriate adaptations at one point along the cardiovascular pathway in order to compare the relative aerobic capacities of different species of mammal. Weibel *et al.* (1991) showed that, when considering adaptive variation in $\dot{V}_{O_{2max}}$ (i.e. the difference between sedentary and athletic mammals of a given body mass) at the level of the convective transport of oxygen by blood, the product of erythrocyte volume and heart stroke volume increased in the athletic species in direct proportion to the increase in $\dot{V}_{O_{2max}}$.

In this regard, Bishop (1997) demonstrated that the maximum stroke volume of mammals can be directly estimated from data for heart mass and that erythrocyte volume can be replaced by haemoglobin concentration to yield an estimate equivalent to the oxygen delivery of the heart per beat. In addition, by assuming that the cardiac muscles of birds are functionally similar to those of mammals, reasonable predictions for the $\dot{V}_{O_{2max}}$ of birds during flight can be made based on data for heart mass and haemoglobin concentration (Bishop 1997). Therefore, it is possible to use published data for relative heart mass and haemoglobin concentration to normalize the measured values for $\dot{V}_{O_{2max}}$ so as to yield predictions for the $\dot{V}_{O_{2max}}$ and aerobic scope of a series of standard birds and mammals. The relative heart mass of birds and mammals is typically between 0.5 and 1.5% of body mass while the average haemoglobin concentration for birds

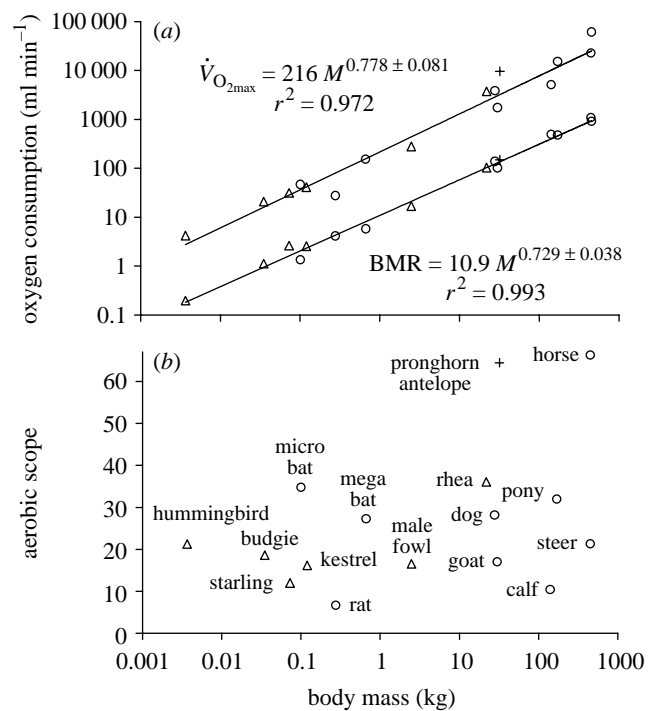


Figure 2. (a) $\dot{V}_{O_{2max}}$ and BMR and (b) aerobic scope plotted against body mass (kg) for nine species of mammal (open circles) and six species of bird (open triangles). The equivalent data for the pronghorn antelope (plus signs) is also plotted, although these data are not included in the regression analysis (see text). Data sources are given in the text.

and mammals is around 15 g 100 ml⁻¹ blood (Schmidt-Nielsen 1984), so I will define a standard bird or mammal as one which has a relative heart mass of 1% of body mass and a haemoglobin concentration of 15 g 100 ml⁻¹ blood.

(b) Calculation of the standard $\dot{V}_{O_{2max}}$ and aerobic scope

I suggest that reasonable estimates of heart mass and haemoglobin concentration (see Bishop 1997) and \dot{V}_{O_2} are available for at least two species of running birds (Brackenbury *et al.* 1981; Bundle *et al.* 1999), four studies of flying birds (Tucker 1968; Torre-Bueno & Larochelle 1978; Gessaman 1980; Wells 1993), two studies of flying bats (Thomas & Suthers 1972; Carpenter 1985) and seven species of running mammals (Gleeson *et al.* 1983; Karas *et al.* 1987; Taylor *et al.* 1987; Jones *et al.* 1989), for which the values for \dot{V}_{O_2} are likely to be maximal. These values for $\dot{V}_{O_{2max}}$ are plotted against body mass in figure 2a along with data for BMR from the same species. The values for BMR were taken from Bennett & Harvey (1987) and McNab (1988) and adjusted for any differences in body mass assuming an intraspecies allometric scaling exponent of 0.67 (Heusner 1982; Feldman & McMahon 1983). All data for $\dot{V}_{O_{2max}}$ and BMR are presented as millilitres of oxygen per minute and were log transformed prior to regression analysis and the calculation of 95% confidence limits using the method of least squares. The results for the calculation of the body mass exponents are presented as means \pm 95% confidence limits. Figure 2a shows that the body mass exponent for $\dot{V}_{O_{2max}}$ was not significantly different from

that for BMR ($M_b^{0.778 \pm 0.081}$ and $M_b^{0.729 \pm 0.038}$, respectively). This is clearly demonstrated when the aerobic scope is calculated for these same species and plotted against body mass in figure 2b. Although widely scattered, the aerobic scope does not scale with body mass and the only major outlier in this sample is the value for the horse. However, using data from McNab (1988) and Lindstedt *et al.* (1991), I have also plotted the BMR, $\dot{V}_{O_{2max}}$ and aerobic scope of the pronghorn antelope (*Antilocapra americana*) to illustrate that certain wild animals appear to be able to match the performance of the domestic horse. Clearly, there is no such thing as a 'typical' bird or mammal in the context of $\dot{V}_{O_{2max}}$ (figure 2a) or aerobic scope (figure 2b) as both these data sets are fairly widely scattered, particularly among the mammalian species.

The relative mass of the heart with respect to body mass ($M_h\%$) can vary tenfold between different species (e.g. the range for the species in figure 2 is 0.28–2.36%). In general, relatively small species of birds have much larger $M_h\%$ s than those of similarly sized terrestrial mammals and this is consistent with the higher average aerobic scope of many small species of birds compared to most small terrestrial mammals such as rodents (Pasquis *et al.* 1970). However, bats have relatively large $M_h\%$ s, relatively high values for haemoglobin concentration and relatively high values for aerobic scope. Larger species of mammals also exhibit a wide range in $M_h\%$ and haemoglobin concentration but the highest values are similar to the highest values found for birds of a similar body mass and this is consistent with the rhea having a similar aerobic scope to that of dogs.

Further regression analysis, of body mass against heart mass followed by a plot of the residuals for heart mass against the residuals for $\dot{V}_{O_{2max}}$, shows that 78% of the variance shown in the residuals for $\dot{V}_{O_{2max}}$ can be accounted for by the variance in the residuals for heart mass. Taking into account the interspecific differences in haemoglobin concentration raises the variance accounted for to 95%. In contrast, a similar analysis conducted on the residuals for BMR shows that differences in heart mass can only account for a maximum of 5% of the variance in BMR. This result justifies the use of relative heart mass and haemoglobin concentration for normalizing the data for $\dot{V}_{O_{2max}}$ but not for BMR.

I have estimated the $\dot{V}_{O_{2max}}$ of standard birds and mammals by dividing the measured values for $\dot{V}_{O_{2max}}$ shown in figure 2a by the factor $(M_h\% \times Hb_{rel})$, where Hb_{rel} is the blood haemoglobin concentration ($g\ 100\ ml^{-1}$ blood) of each species divided by 15 (as the average haemoglobin concentration for all birds and mammals is ca. $15\ g\ 100\ ml^{-1}$ blood). The results for the estimation of the $\dot{V}_{O_{2max}}$ of standard birds and mammals are plotted in figure 3a. This approach dramatically reduces the variance in the values for $\dot{V}_{O_{2max}}$. It shows that the underlying influence of body mass on the aerobic capacity of both birds and mammals can be described by the same equation, i.e.

$$\text{Standard } \dot{V}_{O_{2max}} = 253 M_b^{0.879 \pm 0.020}, r^2 = 0.999. \quad (1)$$

The body mass exponent for the standard $\dot{V}_{O_{2max}}$ is highly significantly different from that for BMR. Figure 3b

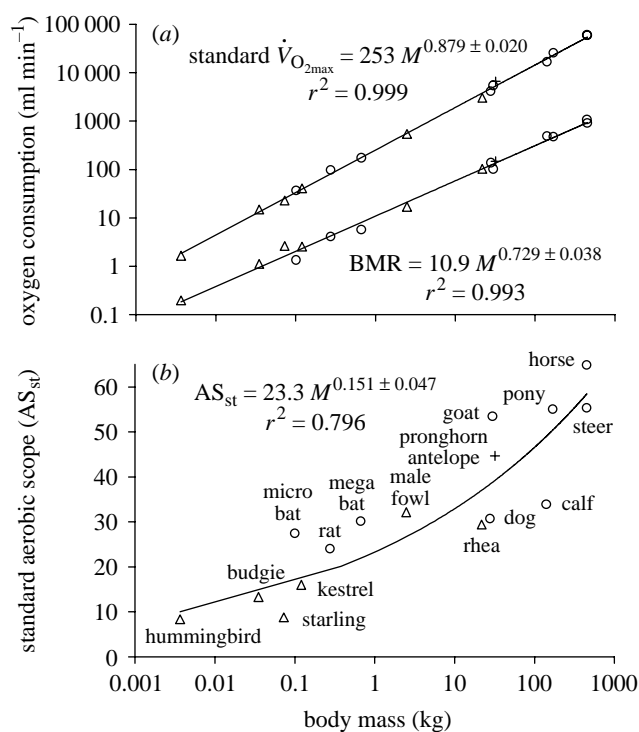


Figure 3. (a) Standard $\dot{V}_{O_{2max}}$ and BMR and (b) standard aerobic scope (see text) plotted against body mass (kg) for nine species of mammal (open circles) and six species of bird (open triangles). The estimated equivalent data for the pronghorn antelope (plus signs) are also plotted, although these data are not included in the regression analysis. The heart mass for the pronghorn antelope is assumed to be 1.4% of body mass (see text). Data are sources given in the text.

shows the same data calculated as standard aerobic scope (AS_{st}) and plotted against body mass. Regression analysis shows that

$$AS_{st} = 23.3 M_b^{0.151 \pm 0.047}, r^2 = 0.796. \quad (2)$$

The body mass exponent of 0.15 for aerobic scope is highly significantly different from zero. Standardizing the data with reference to $M_h\%$ only, produces a similar equation but with a reduced correlation coefficient ($24 M_b^{0.140 \pm 0.062}$, $r^2 = 0.671$). Thus, if all birds and mammals had a heart mass representing 1% of overall body mass and a haemoglobin concentration of $15\ g\ 100\ ml^{-1}$ blood (and all other variables were appropriately adjusted in proportion), then $\dot{V}_{O_{2max}}$ should scale allometrically with an exponent 0.15 ± 0.05 greater than that of BMR.

As heart beat frequency is the only functional variable associated with the convection of blood that scales significantly with respect to body mass (Weibel *et al.* 1991; Bishop 1997), then the maximum heart beat frequency of birds and mammals should scale with a smaller negative exponent than that of the resting heart beat frequency, i.e. $M_b^{-0.12 \pm 0.02}$ and $M_b^{-0.27 \pm 0.04}$, respectively. This compares to the data collated by Bishop & Butler (1995) which showed that the scaling exponent for the heart beat frequencies of birds measured during flight was $M_b^{-0.17 \pm 0.02}$ ($n = 42$), which was significantly different from that measured for birds at rest ($M_b^{-0.33 \pm 0.06}$, $n = 36$; both recalculated as least-squares regressions). The

maximum heart rate of mammals ($n=24$) scales as $M_b^{-0.16 \pm 0.02}$ (Bishop 1997).

3. DISCUSSION

The above analysis suggests that, all other things being equal, the capacity for aerobic scope should be greater in larger species and that the underlying influence of body mass on the exponent for $\dot{V}_{O_{2max}}$ is significantly smaller than that on the exponent for BMR. In addition, the fractal geometry of the blood vascular system might be more appropriately related to $M_b^{0.88}$ rather than to $M_b^{0.75}$. Given a similar relative heart mass, larger athletic animals appear to have the capacity to place proportionally more of their available energy into useful locomotion rather than into tissue maintenance costs. This will have a general significance for related issues of scaling in animal locomotion, such as the relative ability of larger species of birds to sustain flapping flight (Pennycuik 1989). However, this conclusion depends on the assumption that the maintenance costs during exercise are similar to those at rest or that they are in direct proportion to those at rest. This assumption may not be true and would be an interesting area for future research (Pennycuik 1998).

The above relationships and the model of Bishop (1997) can be used to make predictions concerning the aerobic performance or heart mass of other species. For example, the 32 kg pronghorn antelope has a very high mass-specific $\dot{V}_{O_{2max}}$, which is comparable to that of the 0.7 kg megachiropteran bat *Pteropus poliocephalus* and over five times greater than that of a similarly sized goat (Lindstedt *et al.* 1991). The model of Bishop (1997) predicts a relative heart mass for the pronghorn antelope of ca. 1.4% body mass. While this appears to be very large, it would seem to be perfectly feasible. The predicted aerobic scope (based on $M_h\%$ alone) for the largest extant species of terrestrial mammal, a 6654 kg African elephant, would be around 32-fold ($M_h\% = 0.392\%$).

(a) The maximal aerobic performance of birds

How robust are the predictions of avian $\dot{V}_{O_{2max}}$ and aerobic scope based on the similarity of avian and mammalian cardiac muscles? The main problem in answering this question lies in determining the $\dot{V}_{O_{2max}}$ of birds experimentally, particularly as most bird species can probably only achieve maximum metabolic rates during flight (Butler 1991; Nolet *et al.* 1992). In their study of the cursorial rhea, Bundle *et al.* (1999) stated that 'Although the rheas' factorial increase in [aerobic] metabolism is 1.7 times greater than the highest previously reported avian values, we believe that their aerobic scope is representative of birds in general. Previous avian values do not provide evidence of being upper limits; they are probably below species' maxima, but to unknown extents' (p. 31). Thus, Bundle *et al.* (1999) believe that birds in general and, presumably, specifically species of birds which are known to be strong aerobic fliers (such as hummingbirds and budgerigars; see figure 2b) should exhibit aerobic scopes of around 36-fold. In contrast, my analysis suggests that, at the level of the heart and convection of blood and oxygen around the body, the capacity for $\dot{V}_{O_{2max}}$ and/or aerobic scope is similar for birds and mammals and, therefore, that the

current values for the $\dot{V}_{O_{2max}}$ of birds and bats flying in wind tunnels (figure 2) are likely to be maximal (Bishop 1997).

Although only the study of the rhea provided measurements for lactate production, I believe that Bundle *et al.* (1999) were not correct to assume that all previous studies of birds failed to provide evidence of maximal flight performance. For example, the data from the studies of hummingbirds hovering while carrying extra weights (Wells 1993) and hovering in hypodense gas mixtures (Chai & Dudley 1995) showed that these birds reached both their biomechanical and physiological limits as far as sustained hovering flight was concerned, with hovering times reduced to just a few seconds of flight. In addition, the mitochondria of hummingbirds already operate with the highest mass-specific rates of oxygen consumption known for any vertebrate (ca. $10 \text{ ml O}_2 \text{ cm}^{-3} \text{ min}^{-1}$) (Suarez 1992). The data for the budgerigar were obtained from birds flying at 12 m s^{-1} in a wind tunnel with a 5° angle of tilt (Tucker 1968) and, as with most of the data from wind tunnel studies, it proved impossible to train birds to fly faster than the highest speeds published. Similarly, the studies of Carpenter (1985, 1986) showed that bats have only a very limited range of flight speeds over which they can be trained to fly in a wind tunnel before they become exhausted.

The rhea has a relatively large $M_h\%$ of ca. 1.2% of body mass (Magnan 1922; Bundle *et al.* 1999). Using model 2 from Bishop (1997), I obtain a prediction for the $\dot{V}_{O_{2max}}$ of the rhea of ca. 4363 ml min^{-1} (95% confidence interval $3489\text{--}5456 \text{ ml min}^{-1}$) compared to the actual measured $\dot{V}_{O_{2max}}$ of 3728 ml min^{-1} reported by Bundle *et al.* (1999). Thus, the evidence from the data for $M_h\%$ alone would have clearly indicated, with a reasonable degree of accuracy (mean error + 17%), that the rhea should have a very large aerobic scope. The $M_h\%$ s of the phylogenetically and ecologically related ostrich (123 kg) and emu (37.5 kg) are 0.98% (Crile & Quiring 1940) and 0.85% (Grubb *et al.* 1983), respectively, and give predictions for aerobic scope of around 46 for the ostrich and 34 for the emu. Additional data for haemoglobin concentration would improve these predictions.

(b) Submaximal aerobic performance

From the perspective of blood and oxygen convection around the body as a limiting factor for $\dot{V}_{O_{2max}}$, it is critical to include only data from species that are exercising near their $\dot{V}_{O_{2max}}$ with respect to their central cardiovascular adaptations. It is well established for birds that are normally capable of prolonged bouts of aerobic flight that running on a treadmill or swimming on a water flume does not elicit maximum oxygen consumption (Butler 1991; Nolet *et al.* 1992). Thus, the inclusion of data from such species would be invalid in this context (see figure 1; Bundle *et al.* 1999). These submaximal aerobic performances are limited by the respective peripheral muscle aerobic adaptations (such as mitochondrial volume density) and relatively reduced aerobic muscle mass (i.e. of the leg muscles), as supported by the recording of submaximal heart rates during running and swimming (Butler 1991; Nolet *et al.* 1992). In these examples, the argument of symmorphosis would define the leg muscle adaptations as part of a

separate tributary pathway for oxygen delivery as the maximal performance of the cardiac tissue is clearly matched to a different set of peripheral tissues (i.e. the flight muscles). However, it is interesting to note that, even during peripherally limited aerobic exercise, it would appear that there is a trend for larger animals to have greater aerobic scopes (see figure 1; Bundle *et al.* 1999). In principle, if the heart mass and haemoglobin concentration are known, then it should be possible to suggest the degree to which these measurements are submaximal with respect to the centrally limited $\dot{V}_{O_{2\max}}$ and correlate this with parameters such as the heart rate, oxygen extraction efficiency and comparative mitochondrial volumes and muscle masses.

For the majority of terrestrial and flying birds and mammals I would expect that the use of heart mass and haemoglobin concentration for predicting $\dot{V}_{O_{2\max}}$ and maximum aerobic scope will be reasonably accurate. However, certain conditions may arise that could greatly alter the general relationship between the central and peripheral adaptations. One example is the giraffe (Pedley *et al.* 1996) where the heart mass is greatly increased due to the need to have very thick ventricular muscle walls to cope with their unusually high blood pressure. Another possible example might be found in aquatic birds and mammals which are specialized for diving. Heart mass is closely related to blood volume (Spencer 1966, 1967), so it is possible that a diving animal might be selected for a large blood volume and, hence, a large heart mass independently of any peripheral adaptations for aerobic locomotor performance.

In contrast to Bundle *et al.* (1999), I suggest that there is little reason to assume that the current measurements of $\dot{V}_{O_{2\max}}$ from at least six species of birds are likely to be submaximal. Rather, it would appear that, when considering the aerobic scope of different species, it is just as important to consider the measurement and definition of BMR. The value for the BMR of the starling (Bennett & Harvey 1987) appears to be relatively high while the value for $\dot{V}_{O_{2\max}}$ is close to the predicted value. Similarly, the measurements of the $\dot{V}_{O_{2\max}}$ of the two types of bat are reasonably close to the predictions but the data for BMR are relatively low (McNab 1988) and result in a comparatively high and arguably misleading value for aerobic scope. Interestingly, Daan *et al.* (1989) showed that body composition had an important influence on the mass-independent variance of BMR in birds, with heart mass accounting for *ca.* 25% of the residual variance, although this correlation was not found in the present study. As demonstrated by Bishop (1997), there is little difference between the functional performance of avian and mammalian cardiac muscle or in the relative capacity of birds and mammals for $\dot{V}_{O_{2\max}}$ and aerobic scope. At the level of the heart, sedentary or athletic birds are similar to sedentary or athletic mammals, respectively, and there is nothing intrinsically remarkable about the aerobic performance of birds or particularly poor about the aerobic ability of mammals.

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REFERENCES

- Åstrand, P.-O. & Rodahl, K. 1986 *Textbook of work physiology*, 3rd edn. New York: McGraw-Hill.
- Bennett, P. M. & Harvey, P. H. 1987 Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool. Lond.* **213**, 327–363.
- Bishop, C. M. 1997 Heart mass and the maximum cardiac output of birds and mammals: implications for estimating the maximum aerobic power input of flying animals. *Phil. Trans. R. Soc. Lond. B* **352**, 447–456.
- Bishop, C. M. & Butler, P. J. 1995 Physiological modelling of oxygen consumption in birds during flight. *J. Exp. Biol.* **198**, 2153–2163.
- Brackenbury, J. H., Avery, P. & Gleeson, M. 1981 Respiration in exercising fowl. I. Oxygen consumption, respiratory rate and respired gases. *J. Exp. Biol.* **93**, 317–325.
- Bundle, M. W., Hoppeler, H., Vock, R., Tester, J. M. & Weyand, P. G. 1999 High metabolic rates in running birds. *Nature* **397**, 31–32.
- Butler, P. J. 1991 Exercise in birds. *J. Exp. Biol.* **160**, 233–262.
- Carpenter, R. E. 1985 Flight physiology of flying foxes, *Pteropus poliocephalus*. *J. Exp. Biol.* **114**, 619–647.
- Carpenter, R. E. 1986 Flight physiology of intermediate-sized fruit bats (Pteropodidae). *J. Exp. Biol.* **120**, 79–103.
- Chai, P. & Dudley, R. 1995 Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. *Nature* **377**, 722–725.
- Chappell, M. A., Zuk, M. & Johnsen, T. S. 1996 Repeatability of aerobic performance in red junglefowl: effects of ontogeny and nematode infection. *Funct. Ecol.* **10**, 578–585.
- Crile, G. & Quiring, D. P. 1940 A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio J. Sci.* **XL**, 219–259.
- Daan, S., Masman, D. & Groenewold, A. 1989 Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *Am. J. Physiol.* **259**, R333–R340.
- Feldman, H. A. & McMahon, T. A. 1983 The 3/4 mass exponent for energy metabolism is not a statistical artifact. *Respirat. Physiol.* **52**, 149–163.
- Gessaman, J. A. 1980 An evaluation of heart rate as an indirect measure of daily energy metabolism of the American kestrel. *Comp. Biochem. Physiol.* **65**, 273–289.
- Gleeson, T. T., Mullin, W. J. & Baldwin, K. M. 1983 Cardiovascular responses to treadmill exercise in rats: effects of training. *J. Appl. Physiol.* **54**, 789–793.
- Grubb, B. R., Jorgensen, D. D. & Conner, M. 1983 Cardiovascular changes in the exercising emu. *J. Exp. Biol.* **104**, 193–201.
- Hemmingsen, A. M. 1960 Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Rep. Steno Mem. Hosp. Copenhagen* **9**, 1–110.
- Heusner, A. A. 1982 Energy metabolism and body size. I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact? *Respirat. Physiol.* **48**, 1–12.
- Hinds, D. S., Baudinette, R. V., MacMillen, R. E. & Halpern, E. A. 1993 Maximum metabolism and the aerobic factorial scope of endotherms. *J. Exp. Biol.* **182**, 41–56.
- Jones, J. H., Longworth, K. E., Lindholm, A., Conley, K. E., Karas, R. H., Kayar, S. R. & Taylor, C. R. 1989 Oxygen transport during exercise in large mammals. I. Adaptive variation in oxygen demand. *J. Appl. Physiol.* **67**, 862–870.
- Jurgens, K. D., Fons, R., Peters, T. & Sender, S. 1996 Heart and respiratory rates and their significance for convective oxygen transport rates in the smallest mammal, the Etruscan shrew *Suncus etruscus*. *J. Exp. Biol.* **199**, 2579–2584.
- Karas, R. H., Taylor, C. R., Rosler, K. & Hoppeler, H. 1987 Adaptive variation in the mammalian respiratory system in

- relation to energetic demand. V. Limits to oxygen transport by the circulation. *Respirat. Physiol.* **69**, 65–79.
- Kleiber, M. 1961 *The fire of life. An introduction to animal energetics*. New York: Wiley.
- Langman, V. A., Baudinette, R. V. & Taylor, C. R. 1981 Maximum aerobic capacity of wild and domestic canids compared. *Fed. Proc.* **40**, 432.
- Lindstedt, S. L., Hokanson, J. F., Wells, D. J., Swain, S. D., Hoppeler, H. & Navarro, V. 1991 Running energetics in the pronghorn antelope. *Nature* **353**, 748–750.
- Longworth, K. E., Jones, J. H., Bicudo, J. E. P. W., Taylor, C. R. & Weibel, E. R. 1989 High rate of O₂ consumption in exercising foxes: large PO₂ difference drives diffusion across the lung. *Respirat. Physiol.* **77**, 263–276.
- McNab, B. K. 1988 Complications inherent in scaling the basal rate of metabolism in mammals. *Quart. Rev. Biol.* **63**, 25–54.
- Magnan, A. 1922 Les caractéristiques des oiseaux suivant le mode de vol. *A. Sci. Nat. Ser. 10* **5**, 125–334.
- Nolet, B. A., Butler, P. J., Masman, D. & Woakes, A. J. 1992 Estimation of daily energy expenditure from heart rate and doubly-labeled water in exercising geese. *Physiol. Zool.* **65**, 1188–1216.
- Pasquis, A., Lacaille, A. & Dejours, P. 1970 Maximal oxygen uptake in four species of small mammals. *Respirat. Physiol.* **9**, 298–309.
- Pedley, T. J., Brook, B. S. & Seymour, R. S. 1996 Blood pressure and flow-rate in the giraffe jugular vein. *Phil. Trans. R. Soc. Lond. B* **351**, 855–866.
- Pennycuik, C. J. 1989 *Bird flight performance*. Oxford University Press.
- Pennycuik, C. J. 1998 Towards an optimal strategy for bird flight research. *J. Avian Biol.* **29**, 449–457.
- Schmidt-Nielsen, K. 1984 *Scaling: why is animal size so important?* Cambridge University Press.
- Scott, I., Mitchell, P. I. & Evans, P. R. 1996 How does variation in body composition affect the basal metabolic rate of birds? *Funct. Ecol.* **10**, 307–313.
- Shephard, R. J. & Åstrand, P.-O. 1992 *Endurance in sport*. Oxford, UK: Blackwell Scientific Publications.
- Spencer, R. P. 1966 Relative heart size of porpoises. *Science* **152**, 230–231.
- Spencer, R. P. 1967 A blood volume heart weight relationship. *J. Theor. Biol.* **17**, 441–446.
- Suarez, R. K. 1992 Hummingbird flight—sustaining the highest mass-specific metabolic rates among vertebrates. *Experientia* **48**, 565–570.
- Taylor, C. R. & Weibel, E. R. 1981 Design of the mammalian respiratory system. I. Problem and strategy. *Respirat. Physiol.* **44**, 1–10.
- Taylor, C. R., Maloiy, G. M. O., Weibel, E. R., Langman, V. A., Kamau, J. M. Z., Seeherman, H. J. & Heglund, N. C. 1981 Design of the mammalian respiratory system. III. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respirat. Physiol.* **44**, 25–37.
- Taylor, C. R., Karas, R. H., Weibel, E. R. & Hoppeler, H. 1987 Adaptive variation in the mammalian respiratory system in relation to energetic demand. II. Reaching the limits to oxygen flow. *Respirat. Physiol.* **69**, 7–26.
- Thomas, S. P. & Suthers, R. A. 1972 The physiology and energetics of bat flight. *J. Exp. Biol.* **57**, 317–335.
- Torre-Bueno, J. R. & Larochelle, J. 1978 The metabolic cost of light in unrestrained birds. *J. Exp. Biol.* **75**, 223–229.
- Tucker, V. A. 1968 Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* **48**, 67–87.
- Weibel, E. R., Taylor, C. & Hoppeler, H. 1991 The concept of symmorphosis: a testable hypothesis of structure–function relationship. *Proc. Natl Acad. Sci. USA* **88**, 357–361.
- Wells, D. J. 1993 Ecological correlates of hovering flight of hummingbirds. *J. Exp. Biol.* **178**, 59–70.
- West, G. B., Brown, J. H. & Enquist, B. J. 1997 A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.

As this paper exceeds the maximum length normally permitted, the author has agreed to contribute to production costs.

